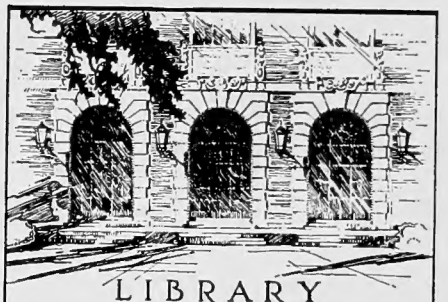

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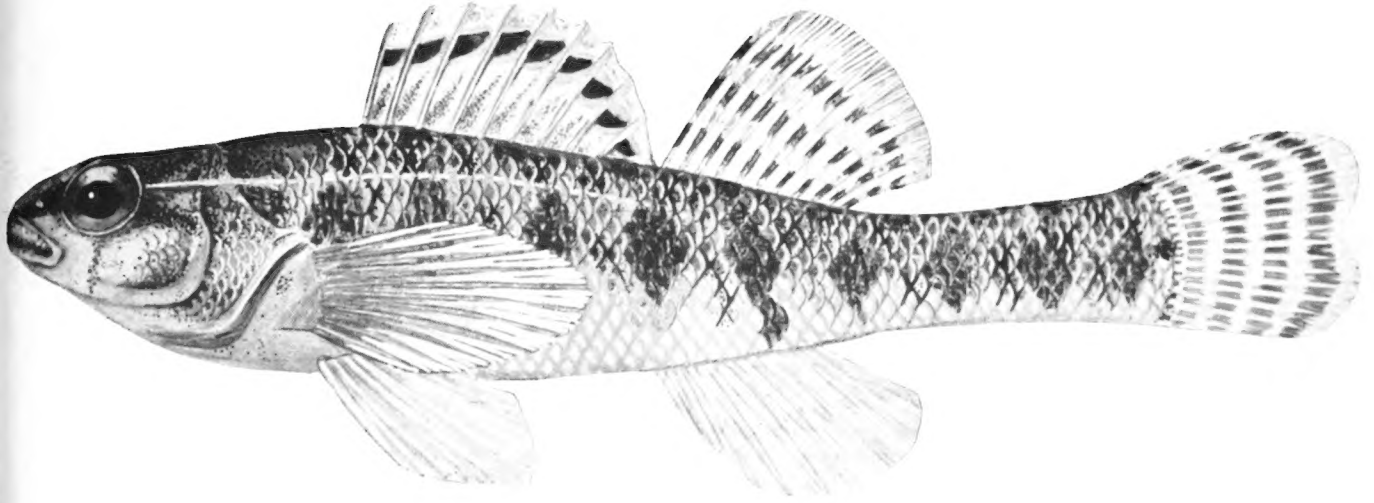

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THE LIFE HISTORY OF THE SLOUGH DARTER, *ETHEOSTOMA GRACILE* (PISCES, PERCIDAE)

Marvin E. Braasch and Philip W. Smith

SEVERAL STUDIES HAVE BEEN PUBLISHED on reproductive habits of darters (for a summary, see Winn 1958). However, a detailed life-history study is not available for any of the eight species and subspecies of the subgenus *Hololepis*. The subgenus is an ecologically distinctive group of which all members typically inhabit swamps, sloughs, and low-gradient streams in the Coastal Plain and Mississippi River valley.

A surprising amount of ecological information has, nevertheless, been assembled by Hubbs & Cannon (1935) and especially by Collette (1962) through remarkably thorough reviews of others' published observations and through inferences drawn from morphology. This paper on the slough darter, *Etheostoma gracile* (Girard), the westernmost member of the subgenus, substantiates many of Collette's (1962) inferences and supplies some missing details.

Etheostoma gracile (cover illustration) is a rather small darter; the adult normally ranges from 35 to 50 mm (1½ – 2 inches) in total length. It shares with other members of its subgenus a highly arched lateral line. The species is unique throughout most of its range in that the lateral line, consisting of 13–27 pored scales, is within three to five scale rows of the base of the spinous dorsal fin.

Females, nonbreeding males, and large young have fine reticulations of brown on the back and sides, overlaying a light yellow or tan. All adult males and most females and large young have green blotches or vertical bands on the sides. In females, nonbreeding males, and large juveniles the spinous dorsal fin is clear, except for a subdistal red-orange stripe or row of red dots; in breeding males the clear area becomes blue black. The soft dorsal and caudal fins are barred with brown; the paired fins and the anal fin are usually patternless.

During the breeding season the male differs from the female in having brighter colors and dark pigment in the basal portion of the spinous dorsal fin. During all seasons the male's genital pore is smaller than its anal pore, but in the female the genital pore is distinctly larger than the anal pore.

The small young of the species can be readily distinguished from juveniles of other darters occurring with them by the distinctly reddish eye, three small caudal spots, and pronounced upward flexure of the groove for the lateral line.

The species was described by Girard (1859:103) as *Boleosoma gracile* (type-locality Rio Seco, Fort Inge, Uvalde County, Texas) and, until Bailey (1951) reduced many nominal genera to subgeneric rank, was variously placed in the genera *Boleosoma*, *Boleichthys*, *Poecilichthys*, and *Hololepis*. *Poecilichthys butlerianus* Hay, 1882 (type-locality Big Black River, Yazoo County, Mississippi) (1882:61) and *Poecilichthys palustris* Gilbert, 1884 (type-locality Switz City swamp, Greene County, Indiana) (1884:209) are junior synonyms.

However, most of the confusion in the literature concerning *Etheostoma gracile* is the result of misidentification of specimens of the superficially similar and allopatric *E. exile* (Girard) and of the closely related and parapatric *E. fusiforme* (Girard). A synonymy, excellent descriptions, and analyses of individual and geographic variation are given by Collette (1962).

The slough darter occurs from the southern portion of Illinois southward in the tributaries of the Wabash and Mississippi rivers through western Kentucky and Tennessee, the bootheel of Missouri, and the state of Mississippi to the Gulf Coast; thence westward through Louisiana and Arkansas approximately to central Texas; and north through eastern Oklahoma to southeastern Kansas (Fig. 1). It is generally distributed and abundant in the southern half of Illinois.

We are indebted to Mark R. Weber, Toshio Yamamoto, David L. Thomas, Arnold Gnilka, Dr. Max Hensley, and Mrs. Dorothy M. Smith for aid in field work; Dr. Hugh B. Cunningham, formerly of the Illinois Natural History Survey, for identification of insect fragments during analyses of stomach contents; and Dr. Francis J. Kruidenier, University of Illinois Department of Zoology, for identification of a fluke parasite. We are also grateful to Mrs. Alice Ann Prickett, formerly of the Illinois Natural History Survey, for executing the drawings and to Wilmer D. Zehr, Survey photographer, for taking photographs of specimens and habitats. The Illinois Natural History Survey provided laboratory facilities and subsidized field work. The manuscript was

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COVER ILLUSTRATION: Adult male *Etheostoma gracile* collected in late November in Johnson County, Illinois. From a watercolor by Mrs. Alice Ann Prickett.

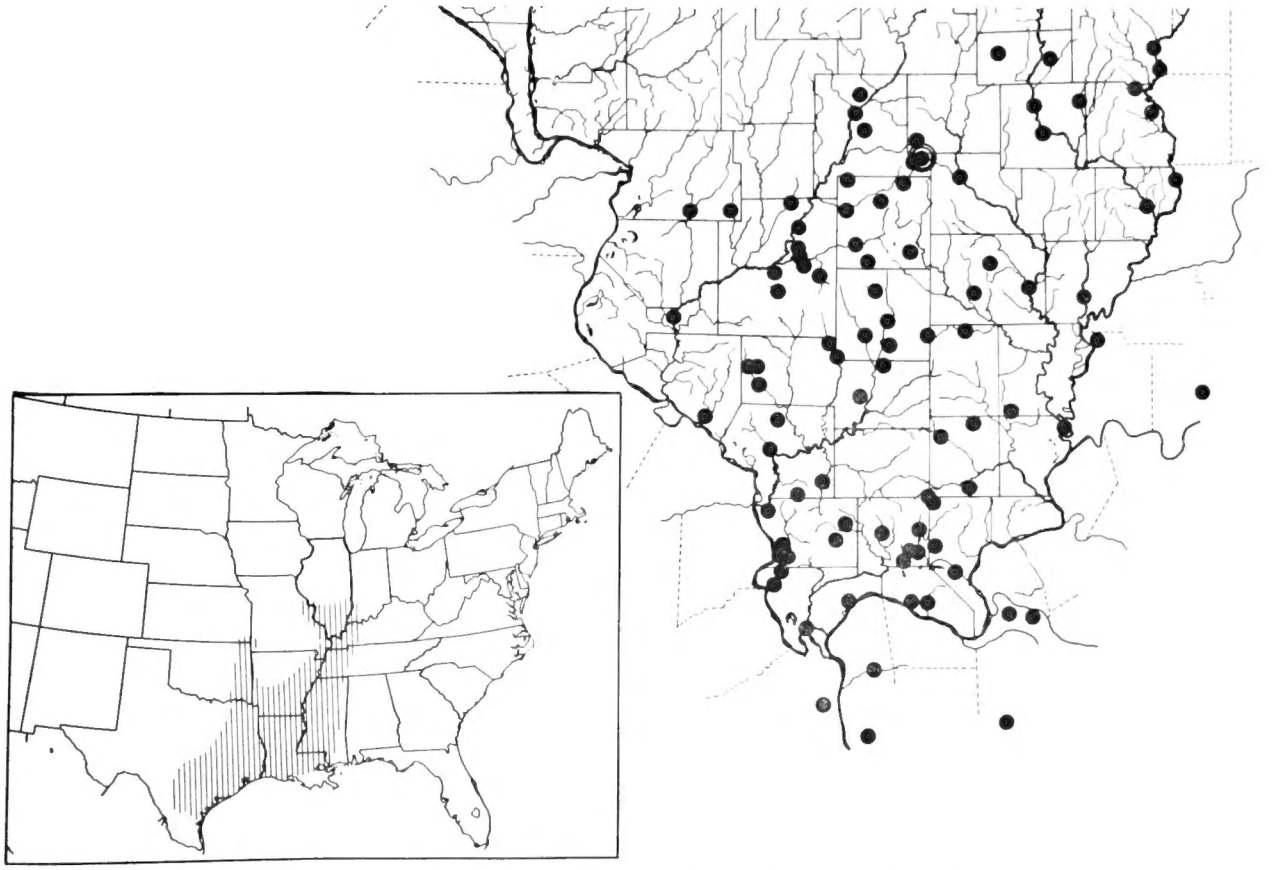

Fig. 1.—Distribution of *Etheostoma gracile* in the upper Mississippi River valley and the total range of the species (inset). The circled dot represents the study area.

edited by Robert M. Zewadski, associate technical editor of the Survey.

Dr. Hobart M. Smith, Professor of Zoology at the University of Illinois, offered helpful suggestions and read the manuscript. Dr. Bruce B. Collette, U.S. National Museum, served as special guest reviewer.

DESCRIPTION OF STUDY AREA

The area selected for study (the circled dot in Fig. 1) is in the vicinity of the Route 37 bridge 1 mile northeast of La Clede, Fayette County, Illinois, a site known to have a large population of slough darters (Fig. 2). The study area is an approximately ¾-mile stretch of Dismal Creek with overhanging vegetation. It extends from the mouth of a temporary tributary west of the highway bridge to the mouth and lower reaches of a semipermanent tributary east of the bridge.

Dismal Creek is a medium-sized stream flowing through dissected clay hills on Illinoian glacial till in the Wabash River watershed. It arises in extreme southeastern Fayette County, flows about 15 miles southeast, and empties into the Little Wabash River in adjacent Clay County near the town of Louisville.

The creek fluctuates greatly in size, depending on the season. In the spring it consists of a few pools up to 20 feet wide and occasionally more than 6 feet deep, each connected by narrow, fine gravel riffles. In the fall these pools are 10 – 15 feet wide and usually no more than 2 – 3 feet deep.

During drought periods the creek is discontinuous, as the water level falls below the level of the riffles and many of the pools stagnate. Some of the pools have sand or clay bottoms; others have bottoms of mud covered with fallen leaves, twigs, and other debris. Because of the variety of bottom types, the stream has a number of microhabitats.

There is considerable pollution from the waste of grazing farm animals. The water temperature (in shade) closely parallels the air temperature, deviating, at least throughout the spring months, no more than 2° F.

METHODS

The study area was visited 23 times from February 14, 1964, to December 12, 1964. Collections were taken at about 2-week intervals in February, March, and April; weekly intervals in May and June; 2-week intervals in July and August; and 4-week intervals from September to December. The specimens collected for study were distributed as follows: February, 53; March, 25; April, 34; May, 6; June, 29; July, 93; August, 35;

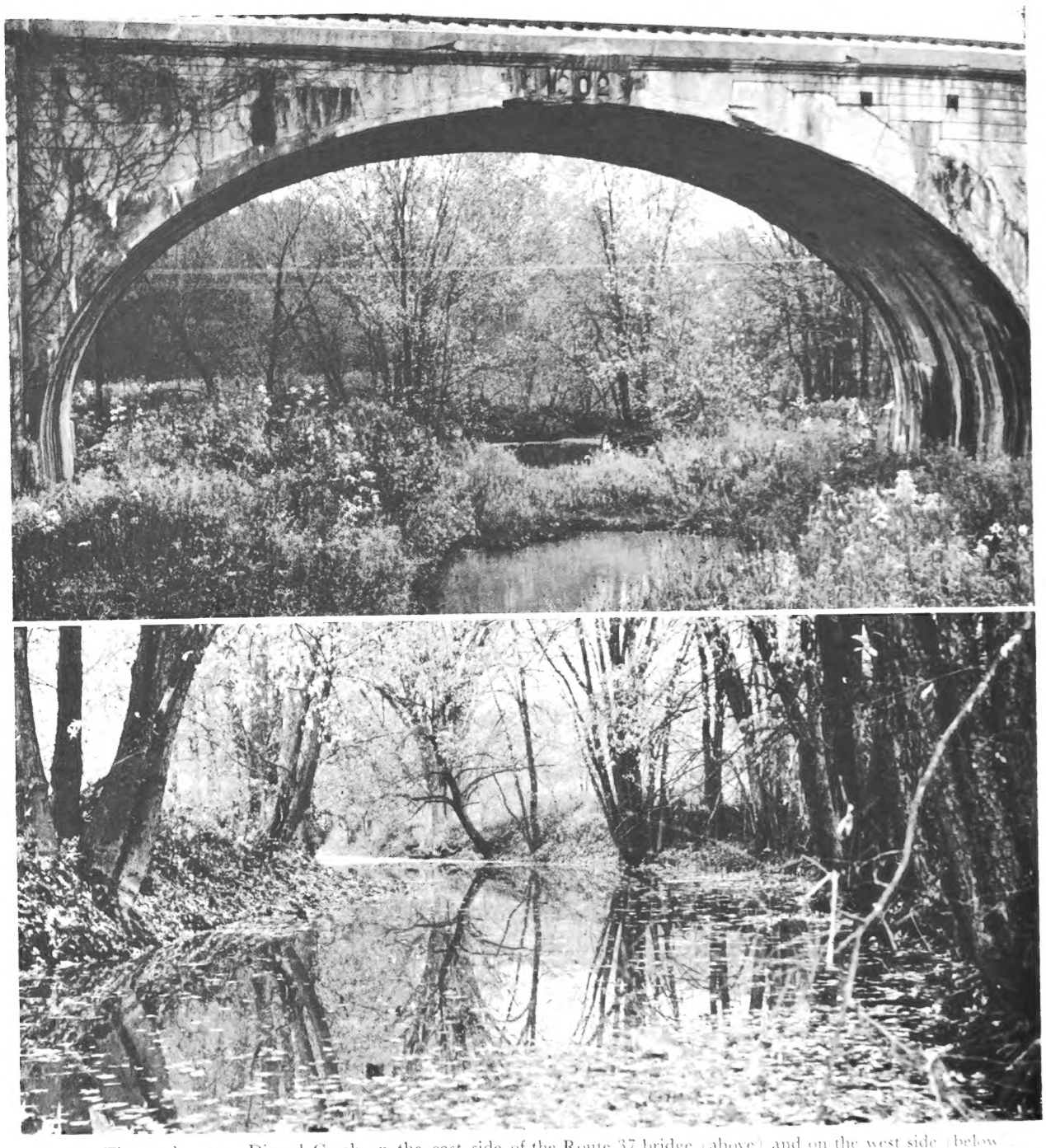

Fig. 2.—The study area. Dismal Creek on the east side of the Route 37 bridge (above) and on the west side (below).

September, 35; October, 38; November, 35; and December, 3.

Supplemental collections made in nearby creeks, particularly during April, May, and June in an effort to determine time of spawning, brought the number of slough darters examined to approximately 400 specimens.

Before spawning time, air and water temperatures were recorded and the stream condition was noted on each visit. Pools over a rather long stretch of creek were sampled with a minnow seine until an adequate sample (10–15 adults) and specimens of various associated species were obtained. Care was exercised to avoid depleting the darter population. Specimens were dropped directly into 10-percent formalin.

As breeding time approached, color photographs were taken of both sexes a day or two after each trip to record color development. A few living pairs were brought to the laboratory in March, April, and May so that their behavior in tanks could be observed.

In May darters became difficult to find, and most of those caught were brought to the laboratory. Spawning could not be observed in the wild because of the high turbidity in the creek, and all spawning observations were made on aquarium fish.

After spawning time fine-mesh screens proved no better than the standard minnow seine in attempts to net hatchlings. For the rest of the year the seining procedure was essentially the same as that used during the prespawning season. However, a much smaller area was sampled to minimize the effects of such variables as air and water temperatures, turbidity, pH, and available food supply. An attempt was made to obtain about 35 young on each visit.

In the laboratory total and standard lengths were recorded for almost all specimens and body depths for adult females. Adults were sexed, aged, and examined for development of color, nuptial tubercles, genital papillae, and numbers of eggs. Specimens were aged by counting annuli on scales removed from the left side of the body above the lateral line near the junction of the dorsal fins.

A few females from each collection were dissected; the color of the ovaries was noted; and egg size, number, and estimated amount of differentiation were recorded. A series from each collection was examined for stomach contents, and parasites were also noted. Young were studied for growth and for development of squamation and the lateral-line system, and the stomachs of a few were examined for food items.

Stomachs of some large, associated species, such as sunfishes, were also examined to see if they were predators of darters. Stomachs of equal-sized species of minnows and other darters were studied for evidence of competition for food.

HABITAT AND ASSOCIATED SPECIES

The microhabitat of the slough darter is quiet or slow-moving water, usually over a soft bottom containing vegetation or debris. In Dismal Creek specimens were collected almost exclusively from mud-bottomed pools, the few exceptions being occasional strays or individuals overwintering in deep sand-bottomed pools when shallower pools were frozen.

Elsewhere, as its common name suggests, the slough darter is most often found in roadside sloughs and ditches. It may also occur in a variety of other habitats, such as springs, slow-moving creeks, small rivers, ponds, oxbow lakes, and backwater pools of very large rivers. In some of these habitats the oxygen content may become low in late summer and fall, although no attempt was made to determine the amount of dissolved oxygen present. For example, in the fall of 1964 Dismal Creek was reduced to a series of stagnant pools and, when the first freeze occurred in December, a heavy fish kill resulted. Most of the slough darters were eliminated, but some were among the few fishes surviving.

Although descriptions of the habitat are scarce, references to the occurrence of the species in Oklahoma (Blair 1959), Indiana (Gerking 1945:95), Illinois (Forbes & Richardson 1920:316), and throughout its range (Collette 1962) suggest that the habitat is similar wherever the species occurs.

An indication of the type of habitat is also provided by the associated species. In Dismal Creek the predominant species are the redfin shiner, *Notropis umbratilis* (Girard); blackstripe topminnow, *Fundulus notatus* (Rafinesque); bluntnose minnow, *Pimephales notatus* (Rafinesque); creek chubsucker, *Erimyzon oblongus* (Mitchill); creek chub, *Semotilus atromaculatus* (Mitchill); golden shiner, *Notemigonus crysoleucas* (Mitchill); striped shiner, *Notropis chrysocephalus* (Rafinesque); longear sunfish, *Lepomis megalotis* (Rafinesque); green sunfish, *L. cyanellus* Rafinesque; pirate perch, *Aphredoderus sayanus* (Gilliams); white sucker, *Catostomus commersoni* (Lacépède); bluegill, *Lepomis macrochirus* Rafinesque; and grass pickerel, *Esox americanus* Gmelin.

In the study area the slough darter is rivaled in abundance by the bluntnose darter, *Etheostoma chlorosomum* (Hay). Other darters present are the blackside darter, *Percina maculata* (Girard); johnny darter, *Etheostoma nigrum* Rafinesque; and orangethroat darter, *E. spectabile* (Agassiz).

REPRODUCTION

The Reproductive Cycle in the Male

In mid-February adult males have already begun to develop breeding coloration. The green or blue-green vertical bands on the sides of some individuals are enlarged and bright, the red spots in the spinous dorsal fin are vivid, and the basal dark pigment is beginning to form. Greater color variation occurs in males than in females, and large 3- and 4-year-old males develop much faster than smaller and younger ones.

By late April the males have reached the peak of coloration. The green bands are brilliant; the spinous dorsal fin is black, except for the subdistal row of bright red dots; and the face and breast are heavily speckled with melanophores. By this time four to six rather large tubercles have formed on the chin (Fig. 3) and numerous minute ones are present on the pelvic and anal fins. There is no noticeable enlargement of the genital papilla or change in size and color of the testes.

By spawning time in late May and early June, the colors have faded somewhat. The timing suggests that colors are used in sex identification and warning away other males while establishing and protecting territories. Lending further support to this inference about the role of color are the absence of color displays during courtship and the spatial separation of males in May. Seldom were two collected near each other then, although in winter several could be taken in one haul. Because of the depth and turbidity of the water in spawning time, territory sizes could not be determined.

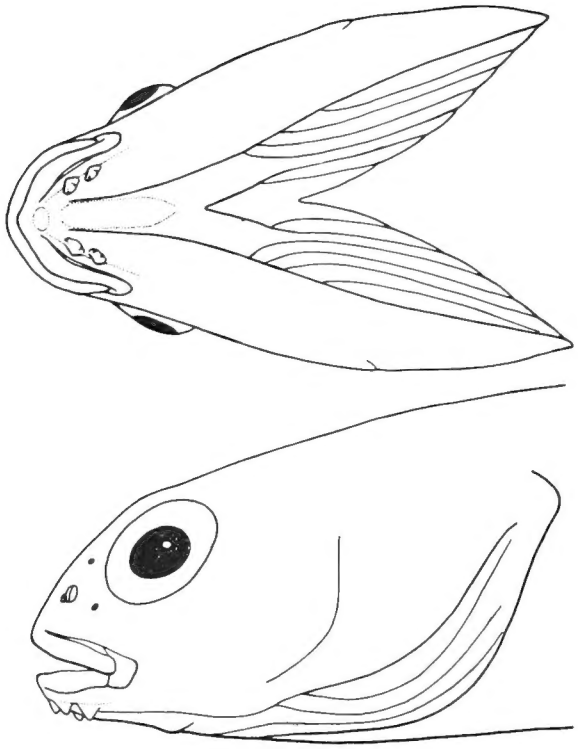

Fig. 3.—Bottom and side views of the nuptial tubercles on the chin of a male *Etheostoma gracile* collected April 10, 1964.

Males, like females, are sexually mature by the spring following their hatching, although at a disadvantage because they are smaller and develop their breeding colors later in the spawning season than do older males. Probably many yearling males do not breed.

Males reach sexual readiness much earlier in the spring than do females. In April males chased and attempted to mount females when placed together in an aquarium, although the females were not ready to spawn for another 1½ months.

The Reproductive Cycle in the Female

The reproductive cycle for the female begins in early November when the first eggs begin to differentiate. Development is slow, and it is not until March that significant growth in egg size takes place. To have some basis for measuring egg development, two observations were made on a few specimens collected from mid-February to early May. First, the percentage of ovarian eggs differentiated was estimated. Although the percentages are based on estimates rather than actual counts, the estimates were consistently made and the percentages are comparable.

The second set of data was gathered by classifying into three categories 100 eggs from a small section excised from the center of the right ovary. The categories are (i) developing but less than 0.33 mm in diameter, (ii) 0.33–0.66 mm, and (iii) over 0.66 mm. Those under 0.33 mm were differentiated but had little appreciable growth, those 0.33–0.66 mm were in the process of maturing, and those larger than 0.66 mm were nearly full size. At spawning, eggs were about 0.85 mm in diameter. The rate of ovarian differentiation and the development of eggs to be laid were rapid during March, April, and May (Table 1).

Table 1.—Rate of differentiation and growth of ovarian eggs in samples of the slough darter collected in Dismal Creek.

Date of Collection	Number of Specimens	Estimated Percent of Eggs Differentiated	Sizes of Differentiated Eggs, Percent		
			Under 0.33 mm	0.33–0.66 mm	Over 0.66 mm
Feb. 14	5	14	61	39	0
Feb. 28	4	36	60	40	0
March 13	5	70	48	45	7
March 30	5	79	42	49	9
April 10	5	92	42	49	9
April 26	5	95	36	53	11
May 8	5	96	30	56	14

A relationship exists between rate of egg maturation and size and age of the fish. Eggs differentiate and mature sooner in older and larger females than in young females. Although the eggs of young females developed slowly in early spring, they actually matured faster in late spring; hence, females of all ages were ready to spawn at the same time.

As the eggs enlarge, the ovaries appear to change color, probably due to yolk and oil formation. In February the ovaries are white, but later become yellow, then yellow-orange as the eggs mature.

As spawning time approaches, the genital papilla enlarges. It begins enlarging in December or January, but the greatest change occurs in February, March, and April. In 2-year-old females the papilla measures 0.9 x 1.1 mm in mid-February but is 1.5 x 2.0 mm by the last of March. The papilla changes shape as it enlarges, developing a bulbous swelling at the base.

After spawning season the eggs remaining in the ovaries atrophy and the female absorbs them. Breakdown begins immediately, and about a month after spawning time the remaining eggs are absorbed, except for the oil droplets, which give the ovaries a bright orange color. By August the ovaries are small and white, except for an occasional yellow spot representing one of the remaining oil droplets. The ovaries have recovered by early November, and the eggs for the next breeding season start to develop.

More than 2,500 eggs are produced in each ovary in one season; however, only about 20 percent ever reach mature size and only a few of these are actually laid.

Mating Behavior and Egg Deposition

The exact stimulus initiating spawning is not known. It apparently is not photoperiodicity or temperature, for fish collected only a few miles upstream from the study area spawned more than a week earlier than those in the study area.

Unlike the females of *E. camurum* (Mount 1959: 241–242) and *Percina peltata* (New 1966:25–26), the female of *E. gracile* is passive to most of the courtship antics of the male. During courtship the persistent male pursues the female and places himself on her back or alongside her with his head above hers. When on top of the female, the male rapidly vibrates his pectoral fins along the female's sides, thus stroking her.

At intervals the male leans forward, opens his mouth very wide, and by bobbing his head rapidly, rubs his chin tubercles over the top of the head and snout of the female (Fig. 4) much as Collette (1962:144) inferred. The male usually also rubs the top of the head and nape of the female with his breast. Sex recognition in the species is evidently good, for no instances of male courting male were noted.

Although the positions of the male's anal and pelvic fins, all of which are tuberculate, were not specifically noted, presumably these fins aid the male in maintaining contact with the female. Collette (1965:605) reported that the male of the allied *E. fusiforme* "beats" the nape of the female with its tuberculate pelvic fins while its tuberculate anal fin remains in contact with the female's caudal peduncle. In *E. gracile* the "beating" seems to be performed by the nontuberculate pectoral fins.

All stimulation by the male is tactile rather than visual. No color displays are made, although the male may become a little brighter, particularly in showing a metallic green around the cheeks and opercles, during pursuit of the female. When the female has been adequately stimulated, she swims to a suitable object, such as a leaf petiole or small twig, makes a pass over it, and fastens a single egg to it.

The male follows closely behind or above and passes over the egg, fertilizing it. The female may make a wide circle, return, and deposit another egg next to the first. In this manner a number of eggs may be placed on one object, usually arranged very neatly and precisely (Fig. 5) although sometimes only one egg is deposited on an object.

The courtship and spawning of *E. gracile* are similar to those described for the related *E. fusiforme* (Fletcher 1957:202–203; Collette 1962:170), but the courting behavior is more elaborate and complex in *E. gracile*.

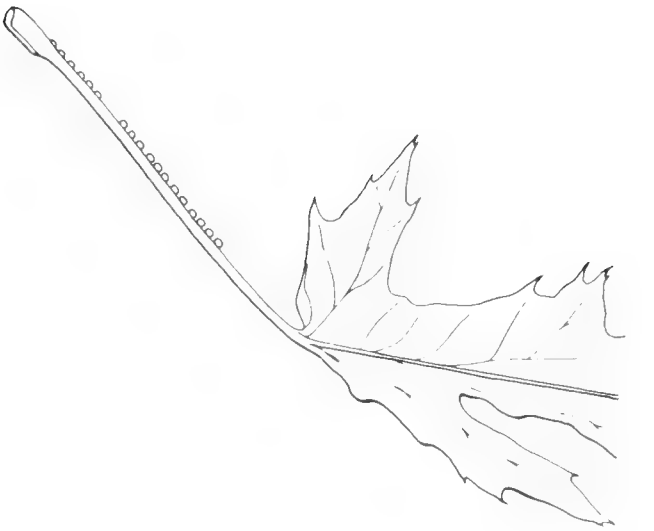

Fig. 5.—Eggs of *Etheostoma gracile* on leaf petiole. Although neatly and precisely arranged, each egg represents a separate pass over the petiole by the parents.

In the laboratory, females laid 30–50 eggs and were not seen spawning more than once each. Whether additional spawning occurs in the wild is not known. No fighting or postspawning care was observed.

Time of Spawning

Eggs were deposited by one female on May 24 or 25, by one on the morning of May 29, and by another on the morning of May 30. No observations could be made in the wild, although the appearance of approximately 1-week-old young upstream from the study area on May 22 suggests that the eggs may have been deposited as early as May 15. Spawning thus occurs in late May in Dismal Creek, the exact time varying from site to site and probably from year to year.

Forbes & Richardson (1920:316) reported full-sized eggs in females taken on April 28. Hubbs & Cannon

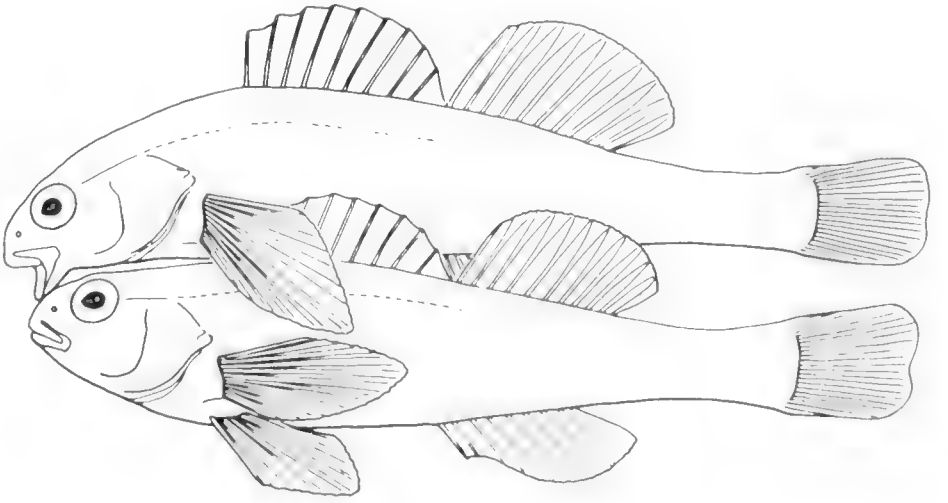

Fig. 4.—Courtship position of *Etheostoma gracile*. At intervals the male "yawns" widely and, by bobbing his head rapidly, strokes the snout of the female with his chin tubercles.

(1935:47) noted that the breeding season in Illinois is late March and April. Collette (1962:144) surmised that in Texas spawning occurs in mid-March. Our data, which indicate a considerably later spawning time, are based on darters at the northern periphery of the species' range and on observations made only in 1964.

Apparently the spawning season is quite short, lasting only 1 or 2 days. Thus, there is little size variation in the hatchlings up to 1 week old at a given site.

HATCHING AND DEVELOPMENT

The egg, reported by Hubbs & Cannon (1935:47) as 1.0 mm in diameter, measured about 0.85 mm in diameter in the Dismal Creek population. Each egg was spherical, except for the place of attachment, a somewhat flattened, opaque disk.

Each egg was clear except for the yellow oil droplet. Eggs deposited either the night of May 24 or the early morning of the 25th showed unpigmented somites by the evening of the 25th and were entirely clear, except for a now-amber oil droplet. By 9 A.M. on the morning of May 26 the large eye and pulsing heart were clearly visible, and the somites had enlarged to fill most of the egg. Three or four large stellate pigment cells were present on the head and fore body, and the oil droplet was proportionately smaller. A few hours later the entire clutch of eggs was lost to mold.

Hatching time in the laboratory for another set of eggs was 5 days at 73° F, the temperature of the stream at that time. The larvae looked like the larva in Fig. 6 and were 2.8 mm in total length. Development is thus more rapid in *E. gracile* than in other species of darters studied. Winn (1958:182) reported a hatching time of 5.5–8.0 days in *E. nigrum* and longer periods for 12 other species. Fahy (1954:185–186) found a hatching time of 18 days for *E. blennioides*. Hatching time obviously varies with the species and water temperature.

Although hatchlings approximately 3 mm in total length were first noted in the laboratory on June 4, two juveniles collected in Dismal Creek on May 22 had already attained standard lengths of 14 and 16 mm (Table 2). On June 11 only two juveniles, measuring

TABLE 2.—Standard length frequencies of Dismal Creek *Etheostoma gracile* collected and preserved February 14–December 12, 1964.

Standard Length, mm	Collection Dates																			
	Feb. 14	Feb. 28	March 13	March 30	April 10	April 26	May 8	May 22	June 4	June 11	June 18	June 25	July 3	July 18	July 31	Aug. 15	Sept. 3	Oct. 1	Nov. 5	Dec. 12
48			2																	
47			..																	
46			..																	
45			..																	
44			..			1														
43			..		1	..									1					
42	1		1	2	..	..				1					..					
41	1		..	..	..	4				..		1			..					
40	1	1	..	..	1	2	1			..		1			..					
39	2	3	2	1	4	1	1			..		..			..					
38	2	6	3	2	3	3	..			..		2			..					
37	3	4	2	2	2	3	1			..		..			..					
36	5	3	1	2	2	1	..			..		..	1		..					
35	5	2	1	1	..	3	1			..		..	..		..				2	1
34	..	..	1	2	..	1	2			..		..	..		..			1	1	..
33	..	1	1	..	..			1*		..		..	..		..			2	9	1
32	2	1		..	1			1*		..		1	..		..			4	4	..
31	..	1		1				..		..		..	..		..		1	3	4	..
30	..	..						..		..		..	..		..		10	10	4	1
29	1	1						..		..		..	..		..	2	3	4	7	
28	1							..		..		..	..		1	4	6	4	2	
27	1							..		..		..	..	1	..	3	3	7		
26								..		..		..	..	2	5	6	6	2		
25								..		..		1	2	2	4	4	2			
24								..		..		3	1	3	5	7	2			
23								..		..		1	5	1	6	3	1			
22								..		..		3	3	3	6	2	2			
21								..		..	1	3	7		2					
20								..		1	1	4	6		1					
19								..		..	..	1	3		2					
18								..		..	1	4								
17								..		..	1	..								
16								1*		1	..	1								
15								..			1									
14								1*												
3									1†											

* Sample consisting of two adults and two hatchlings from a pool several miles upstream from study area.
† Total length of a laboratory-hatched specimen approximately 4 hours old.

16 and 20 mm in standard length, were collected, but by June 18 and thereafter juveniles were fairly numerous and exhibiting growth. Hatching time thus appears to be in late May and early June at this latitude.

It was not possible to rear any fry in the laboratory; thus, all observations on growth of young were made on specimens collected from the study area. At about 7 days of age the young fry had attained many of the adult features. Body proportions were essentially those of adults; eyes, mouth, and, presumably, the digestive tract were fully developed, and fins were present. Squamation was variable, the smaller specimens having fewer scales. In our smallest (14 mm in standard length, not depicted) scales had developed on the sides but not on the belly, back, or opercles. The sensory canals of the head were forming, but the opercular spine had not appeared. Pigmentation features were present, though not as discrete and prominent as in adults, and the dark "teardrop" under the eye was still lacking. The three caudal spots were distinct.

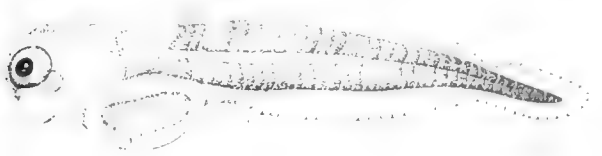

Fig. 6.—Hatchling 2.8 mm in total length, approximately 4 hours old.

Inasmuch as the average size of a 1-year-old *E. gracile* is 30 mm in standard length, the young fish had attained almost half of their 1st year's growth in about 1 week.

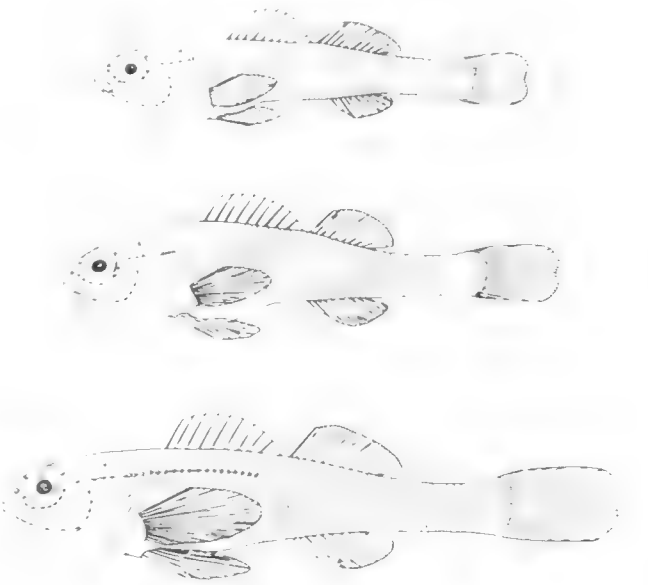

Fig. 7. Development of squamation, lateral-line system, and sensory pores of *Etheostoma gracile*, as illustrated by juveniles of 17, 20, and 25 mm in standard length.

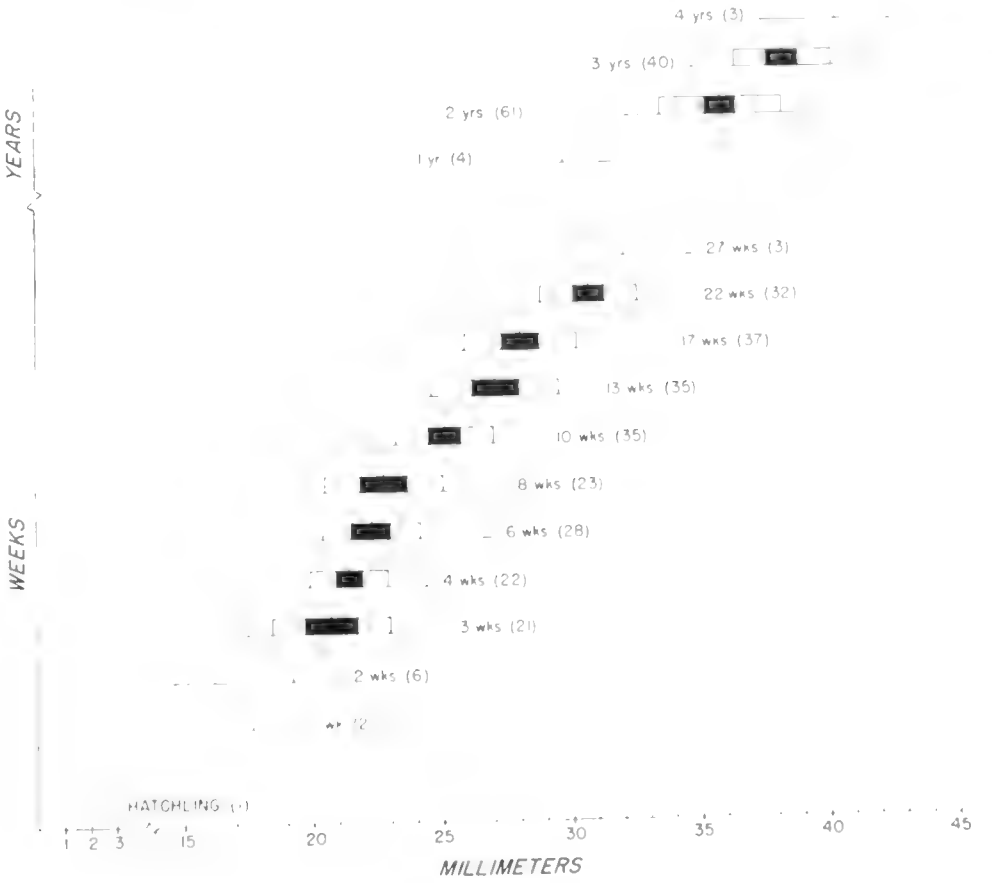

Fig. 8.—Growth of *Etheostoma gracile* in millimeters standard length (except for hatchling, whose total length is shown). In each case the horizontal line represents range; the vertical line, mean; the hollow rectangle, one standard deviation to either side of the mean; and the black rectangle, two standard errors to either side of the mean. Numbers in parentheses are specimens measured.

Collette (1962:139) examined specimens between 12.5 and 14.9 mm (presumably total length) that had not yet developed pored lateral-line scales and specimens between 15.9 and 17.1 mm that had one or no pored scales. Our smallest specimen (14 mm in standard length) had two or three pored scales anteriorly, but another specimen (17 mm in standard length) lacked them. Evidently pored scales first appear at an average total length of about 15 mm and at an age of slightly less than 1 week.

After about 2 weeks the lateral-line pores ranged from 15 to 18, nearly the full complement; an adult may have as few as 13 but usually has 20—23. Squamation was nearly complete; scales were lacking only on the nape and, in some juveniles, on the opercles. The head canals in larger juveniles were complete except for the supratemporal canal, which may require many months to form and sometimes never completely closes. In the 14-day-old darters the subocular canal was complete except for one small interruption.

At the end of approximately 3 weeks squamation was complete, and the opercular spine had formed.

After 1½ months the green pigment had formed on the sides, and the subdistal row of red dots had appeared in the spinous dorsal fin; the females could be sexed by their characteristic genital papillae. The fish at this age are miniature adults.

The development of squamation, the lateral-line system, head pores, and adult bodily proportions are illustrated in Fig. 7.

The growth rate of the slough darter follows the typical sigmoid pattern with the most rapid growth shortly after hatching (Fig. 8). Growth presumably continues throughout life but at a slower and slower rate. There is little indication of sex influence on size. Although the largest specimen collected was a male, the means for the sexes at various ages were usually similar. The young are sexually mature at the end of the 1st year.

PHYLOGENETIC RELATIONSHIPS

The habits and reproductive cycle of *E. gracile* clearly represent an evolutionarily advanced stage. Its habitat and place of egg deposition are similar to those reported for *E. exile* (Winn 1958:160—161). However, its sexual dimorphism, spawning position, place and manner of oviposition, number of eggs, late spawning time, short breeding period, rapid development, and lack of parental care all indicate a greater degree of specialization than in *exile*.

These characteristics also indicate more similarities with the reproductive pattern of *E. microperca*, a darter that occupies a similar habitat and is in the subgenus *Microperca*, than with those of other species discussed by Winn (1958). Differences in size of adults, type of sexual dimorphism, egg size, place of oviposition, and hatching time are relatively minor between the subgenera *Hololepis* and *Microperca*. Collette (1965:605) postulated a close relationship between the two groups because of similar patterns of breeding tubercles.

POPULATION COMPOSITION

During late winter and early spring adults were easy to collect, as they tended to be concentrated in winter aggregations in deep sand- or mud-bottomed pools. In late spring they became scarce and apparently scattered. On a few occasions no adults could be found in the study area, and they remained scarce after the spawning period. In fact, only two adults were taken after July 1 although no great time or effort was expended trying for adults in the postspawning season. The postspawning population in the study area consisted predominantly of young-of-the-year. By early July when the young had become large enough to be seined, the species was again abundant. A series of 30—35 young could be secured with a few short seine hauls. A severe fish kill in early December terminated the study when a sudden cold spell following drought froze the reduced and stagnating pools.

The prespawning population ranged in age from those approaching 1 year to 4 year olds. In the sample taken from the study area from February to April, 1964, 2-year-old fish (year-class of 1962) made up 57 percent of the population, and 2- and 3-year-old fish together constituted 94 percent of the darters taken (Table 3). However, the age composition may vary from year to year.

TABLE 3.—Distribution of sexes and age classes in the samples of the prespawning population collected from the study area.

	Age Class				
Sex	1 year	2 years	3 years	4 years	Total
Male	2	25	22	2	51
Female	2	37	18	1	58
Total	*4*	*62*	*40*	*3*	*109*

The distribution of age classes in the prespawning population sample points out the vulnerability of short-season spawners to such conditions as unusually high or low water levels during the spawning period. Of the 109 adults preserved (some adults were kept alive) in the 3-month period, only four fish were 1 year old, suggesting that the 1963 spawning was only partially successful. Only three fish were 4 years old (year-class of 1960), suggesting that 1960 may also have been a poor year for spawning success. Whether *E. gracile* attains an age of more than 4 years is not known, but it is likely that individuals 4 or more years of age normally make up a very small percentage of the population.

It appears that the physical habitat is the principal enemy of the species, even with its wide range of tolerance, and that changes in the habitat probably control the population level.

The prespawning sample of the population had approximately a 1:1 sex ratio (Table 3), and there was no indication of a difference in longevity between males and females.

FOOD HABITS

Forbes (1878:75) noted "larvae of gnats and of May-flies, with a few copepoda" in the stomach of a specimen of *Boleichthys elegans* (= *E. gracile*) and later (1880:24) reported that three specimens contained 37 percent dipterous larvae and 63 percent ephemerid larvae.

Stomachs of 61 adult slough darters from the study area, taken in February, March, April, May, and June, and of seven juveniles, taken in June, July, September, October, and December, were examined. The types of food eaten, seasonal changes in feeding habits, and differences in food preference between adults and young were noted. Stomachs of a few adults from localities outside the study area, taken chiefly in late summer, were also examined.

During late winter adults fed primarily on midge larvae (Chironomidae) and microcrustaceans, especially copepods and cladocerans (Table 4). The only other item in the stomachs of adults collected in February was the snail (*Lymnaea* sp.). Midge larvae constituted 64 percent by volume of the food eaten in February. Copepods, although more abundant numerically, made up only 21 percent by volume of the stomach contents.

TABLE 4.—Stomach contents of adult slough darters in Dismal Creek, estimated percentages* of each item by volume. Figures in parentheses represent numbers of stomachs examined.

Organism	Feb. (20)	March (20)	April (10)	May (8)	June (3)
Midge larvae	64.1	79.6	55.2	41.2	50.0
Copepods	21.2	13.7	23.2	1.2	50.0
Cladocerans	13.1	1.0	4.7	0.8	...
Aquatic snails	1.5	...	...	...	...
Mayfly larvae	...	3.7	15.4	56.0	...
Amphipods	...	1.0	0.7	0.4	...
Ostracods	...	0.5	0.2	...	...
Fungus fly larvae	...	0.5	...	...	...
Diving beetle larvae	...	...	0.3	...	...
Fairy shrimp	...	...	0.3	...	..

* Rounded to nearest tenth of 1 percent.

In the spring new food organisms were added as they became available. They included other crustaceans (ostracods, amphipods, and phyllopods) and insect larvae (Ephemeroptera, the dipteran Sciaridae, and the coleopteran Dytiscidae). By May mayfly larvae were the predominant food, accounting for 56 percent of the volume of stomach contents, and midge larvae made up 41 percent.

After spawning season the amount of food taken by adults decreased sharply. Stomachs of a few adults from localities outside the study area were examined in July, August, and September. Each was either empty or contained only one food item, and stomachs of all adults were greatly shrunken. Whether reduced feeding is the result of a small food supply or reduced activity brought on by heat and low oxygen availability is not known.

Although very young darters probably feed on diatoms and other plankton, they quickly grow large enough to take adult-sized food. Within 2 weeks the young were eating midge larvae and microcrustaceans, items which furnish most, if not all, of the food of the juvenile fish. The juveniles can eat items of surprisingly large size. For example, a darter 18 mm in standard length collected on July 3 contained a 16-mm midge larva and two copepods.

The greatest volume of food is apparently taken by adults during the spring months, for at that time most of the darters had stomachs greatly enlarged and sometimes containing 60–70 organisms of various sizes. The second greatest volume was found in darters collected in winter, and the smallest in adult darters taken in summer and fall. In contrast, Fahy (1954:152) found that adults of the riffle-inhabiting *E. blennioides* eat least in the winter months and most in July and August.

The main criteria for *E. gracile* appear to be sizes of prey items and their availability. Almost any insect larva small enough to be ingested will be eaten, and even adult darters take such minute food items as copepods and ostracods.

INTERACTIONS WITH OTHER ORGANISMS

Competition

Interspecific competition for food does not seem to be an important factor in the control of population density. Stomachs were removed from two or three specimens of 18 of the 23 associated species in the study area, and their contents were examined for similarities in food types and sizes to those of the slough darter. Like the slough darter, its associates showed no predilection for specific foods.

In Dismal Creek only the bluntnose darter, *E. chlorosomum*, seemed to be in direct competition for food with the slough darter throughout the year. Adults of most other fishes fed on larger organisms in the summer and ate little or nothing in the winter. The young of several species of minnows, darters, and sunfishes, however, did feed on similar items. If there is competition, it does not last long, for the rapidly growing young of larger species quickly switch to larger foods. There is, moreover, a depth separation; darters feed on the bottom, but most minnows, topminnows, and sunfishes feed above the bottom or near the surface.

Ethcostoma spectabile and *E. nigrum* eat the same general types of food, but there is a habitat segregation. *E. spectabile* inhabits a substrate of gravel or rocks, and *nigrum* usually occurs in sand-bottomed or hard-bottomed pools. During the winter all four species of darters retreat to the deeper pools, where they, along with

Percina maculata, may possibly compete for the common food supply.

Although the spawning sites of some of the species associated with the slough darter are not known, there appeared to be no interspecific competition for spawning sites. *Ethcostoma chlorosomum* presumably has the same spawning habitat, but it appears to breed several weeks before *E. gracile*.

Predation and Parasitism

The slough darter, occupying water of usually high turbidity in Dismal Creek, seems to be rather free from predation. Its quick movements and reluctance to move far from cover make it more difficult to catch than minnows, topminnows, tadpoles, and small crayfish, all of which abound in Dismal Creek.

In the stomach analyses of sunfishes and other potential predators from Dismal Creek no darters of any kind were found; however, specimens of both *E. gracile* and *chlorosomum* were taken from the stomach of a warmouth, *Chaenobryttus gulosus* (Cuvier), from a stream in Perry County, Illinois. It is likely that predation pressure on the slough darter depends on the availability of other, more easily caught species.

In other streams predation may be important in controlling population size. Collette (1962:169) cited a series of earlier papers indicating that the related *E. fusiforme* is quite vulnerable to predation by *Esox niger* Lesueur and *Micropterus salmoides* (Lacépède), and one observation that 25 percent of the food of young *Esox niger* consisted of *Etheostoma fusiforme*.

Although no special effort was made to study parasitism, casual observations were made on parasites during the routine examination of specimens. The slough darters in Dismal Creek had an extremely high incidence (approximately 90 percent) of parasitism by a small fluke, *Crepidostomum ?isostomum* Hopkins (family Allocreadiidae). Darters presumably are infected by the intermediate host, a mayfly nymph.

This fluke has previously been known from the logperch, *Percina caprodes* (Rafinesque), and the trout-perch, *Percopsis omiscomaycus* (Walbaum), fishes that also live on mud bottoms of quiet pools. Certain slough darters, when examined, had three or four flukes in the stomach and intestine, but none of the parasitized darters appeared emaciated, weak, or otherwise in bad condition. An occasional nematode was found; the rate of infection was probably less than 1 percent.

Slough darters from other localities sometimes are parasitized by the ectoparasitic copepods (Siphonostomata, probably Lernaeidae). Collette (1962:169–170) commented that glochidia and acanthocephalans on and in *E. fusiforme* were the only parasites of the subgenus *Hololepis* known at the time of his work on the group.

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